

LANDSCAPE BIOACOUSTICS ALLOW DETECTION OF THE EFFECTS OF HABITAT PATCHINESS ON POPULATION STRUCTURE

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Abstract. Landscape structure may affect individual dispersal abilities, thus influencing the genotypic and phenotypic composition of populations. We analyzed the interplay among landscape, behavior, and evolutionary processes by correlating habitat patchiness to the variability in vocalizations of Dupont's Lark *Chersophilus duponti*, one of the most habitat-selective and rare European songbirds. We tape-recorded males throughout the species distribution in Spain, analyzed the spatial patterns of territorial call variation at different scales (individuals, populations, and broad geographic areas), and related acoustic variability to patterns of isolation by geographic distance and by landscape unsuitability (calculated by building a predictive model of habitat suitability). The differentiation of spectro-temporal call features resulted from both isolation by distance and isolation by landscape unsuitability mechanisms. Landscape connectivity was often a better determinant of call differentiation than simple straight-line distance between individuals, providing the first evidence that call transmission can be limited by the presence and distribution of patches of adequate habitat, which likely mediates bird dispersal. Landscape patchiness resulted in a reduction of acoustic diversity (repertoire size) within populations, and a parallel increase in differentiation among populations. Landscape bioacoustics can represent a promising tool for estimating population structure, although the study of animal communication cannot be viewed as an alternative, but a source of complementary information to genetics, given that it provides evidence of male–male transmission and social and cultural phenomena that are currently undetectable from molecular data.

Key words: animal communication; *Chersophilus duponti*; dispersal; Dupont's Lark; fragmentation; landscape connectivity; least-cost distance.

INTRODUCTION

In a context of rapid landscape change and deep concern about diversity loss, understanding how landscape fragmentation affects and structures natural populations is important for improving ecological knowledge and defining optimum strategies for conserving threatened species (Pearman and Wilbur 1990, Diniz-Filho and Telles 2002, Manel et al. 2003). The effects of fragmentation on population structure and dynamics are not merely due to the loss of suitable habitat. Features such as matrix composition, distance between fragments, and patch size complement the effects of habitat loss, especially in highly fragmented landscapes (Andrén 1994). Patch size and isolation do affect animal dispersal, which in turn influences the distribution, abundance, persistence, and structure of populations, as well as the amount of gene flow and the magnitude of genetic diversity (Hitchings and Beebee 1998, Serrano and Tella 2003, Driscoll 2004, Keller et al. 2004). In this framework, the emerging discipline of landscape genetics aims at identifying the spatial genetic patterns related to landscape variables, using genetic data to infer individual dispersal distances when a direct

measure is logistically unfeasible (Manel et al. 2003). When no previous knowledge exists on the grouping of individuals within subpopulations, the classic approach implies the assessment of the associations between individual relatedness (or differentiation) and the geographic distance between them. Under isolation by distance mechanisms (sensu Wright 1943), gene flow occurs step by step, with individuals at increasing distances being progressively less genetically close. In heterogeneous and fragmented landscapes, however, connectivity between patches may affect gene flow much more than the simple straight-line distance between them (Arnaud 2003, Coulon et al. 2004).

Despite the increasing interest in the links between landscape and genotypic traits, there is still scarce empirical evidence of the association between landscape structure and the phenotypic composition of populations. The phenotypic consequences of landscape fragmentation have been investigated by focusing on wing shape (Taylor and Merriam 1995) and biochemistry of flight muscles of insects (Hanski et al. 2004), traits which have a direct connection with movements and dispersal. Conversely, links among dispersal, landscape geometry, and acoustic communication are less immediate, although dialects are a well-documented effect of spatial isolation processes (Barbujani et al. 1996, Wright

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1996, Peake and McGregor 1999). Dialects can reflect population genetic structure (Backer 1982, Barbujani and Sokal 1989, MacDougall-Shackleton and MacDougall-Shackleton 2001), although dialect and genetic boundaries do not always match (Lougheed and Handford 1982, Zink and Barrowclough 1984). This mismatch originates from the dual nature of communication systems, which can develop from the interaction between genes and environmental components in a social and cultural context. "Songs" (long and complex utterances) of oscine birds represents a well-known example of learned vocalizations, whereas the environmental influence can be less relevant in "calls" (briefer and simpler sounds) (Thorpe 1958). We can expect discordance between vocal and genetic data when local dialects are learned by immigrants after rather than before dispersal (Wright et al. 2005). The cultural component of communication systems, however, does not prevent vocalizations being affected by isolating mechanisms such as anthropogenic habitat loss, which reduces the transmission of cultural traits by separating populations or individuals (Holland et al. 1996, Laiolo and Tella 2005).

Here we correlate landscape patchiness to the variability in calls of Dupont's Lark (*Chersophilus duponti*), one of the most ecologically as well as geographically restricted and endangered European songbirds. The world distribution of this species is reduced to fragmented areas of Spain and northern Africa (Cramp 1988, Garza et al. 2003a). This is a terrestrial, mostly insectivorous bird that exclusively inhabits the flat patches of natural shrub-steppes, habitats that have been greatly reduced and fragmented by agricultural intensification (Garza et al. 2003a). Historical and recent landscape changes provoked the population and range contraction of this species in southern Europe (Cramp 1988); the species is now confined to Spain, with an estimated population size of 1300–1900 territorial males distributed among a number of patches of suitable habitat varying greatly in geographic distribution, size, and isolation (Garza et al. 2003a, b, Tella et al. 2005). Due to the patchy and scattered nature of its distribution, Dupont's Lark can be used as a model to test for the effects of spatial isolation on population diversification.

Larks (Alaudidae) are well known for their complex song performances that often incorporate imitations of other birds (De Juana et al. 2004). Dupont's Lark's song is long and extremely variable, whereas the calls are quite simple and conservative throughout the species' western range (Morocco and Spain) (Laiolo and Tella 2005, Laiolo et al. 2005). Here we address the brief and stereotyped territorial call. We tape-recorded males throughout the species' distribution in Spain, with the aims of analyzing (1) the spatial patterns of call variation at different scales (individuals, populations, and broad geographic areas), (2) the acoustic variability in relation to isolation by geographic distance, and (3) the acoustic variability in relation to isolation by

landscape unsuitability. The latter was quantified by using a predictive model of habitat suitability built ad hoc for this study. We eventually discuss the use of a behavioral trait (communication system) to infer population structure and detect the effects of landscape fragmentation on dispersal behavior as an alternative or complement to molecular data.

METHODS

Study areas and sound recordings

Dupont's Lark inhabits five topographic areas of the Iberian Peninsula: the Iberian Mountains, Ebro Valley, Southern Plateau, Northern Plateau, and Southern Spain (Fig. 1). Despite their close proximity, these broad geographic areas differ greatly in topography and climate. The Iberian Mountains, in the elevation range of 800–2000 m a.s.l., are composed of northwest-to-southeast oriented rocky massifs and slightly undulating reliefs separated by deep valleys; the Ebro Valley is a wide, dry plain at 200–500 m a.s.l.; Northern and Southern Plateaus are high plains mainly located at 600–1000 m a.s.l.; Southern Spain includes the Betic-Penibetic systems that face the Mediterranean coast. The ridges of the Iberian and Central Mountains separate the Ebro Valley, Northern, and Southern Plateaus, whereas altitudinal differences separate the Iberian Mountains from neighboring areas. There is a gradient of decreasing abundance of Dupont's Lark across this range, with The Iberian Mountains hosting the bulk of Spanish populations, and the Northern Plateau and Southern Spain comprising a few small (<20 territories) and isolated populations (Garza et al. 2003a, Tella et al. 2005).

Patchiness of Iberian shrub-steppes derives from both natural patterns and anthropogenic processes, the latter component becoming relevant in the last decades as a consequence of agricultural development (Tella et al. 2005; P. Laiolo and J. L. Tella, *authors unpublished data*). The anthropogenic contribution to fragmentation is relevant at the area level (i.e., within areas), whereas natural barriers mostly separate areas (i.e., among areas). As all the analyses were carried out at the area level, we can state that human intervention played an important role in landscape patchiness, although natural and anthropogenic patterns cannot easily be separated.

The five areas were delimited by ellipses of similar size and considered as the five geographic units used for building a predictive model of habitat suitability and further spatial analyses. We defined "populations" within these areas as patches or groups of nearby patches inhabited by the species and largely isolated from others; we based this definition on the apparently scarce interpatch movements of this species, as derived from radiotelemetry and systematic observations of color-banded birds (Garza et al. 2005; M. Vögeli, D. Serrano, and J. L. Tella, *unpublished data*). Dupont's Lark distribution outside the five delimited areas is restricted to 6–7 territories from one locality in

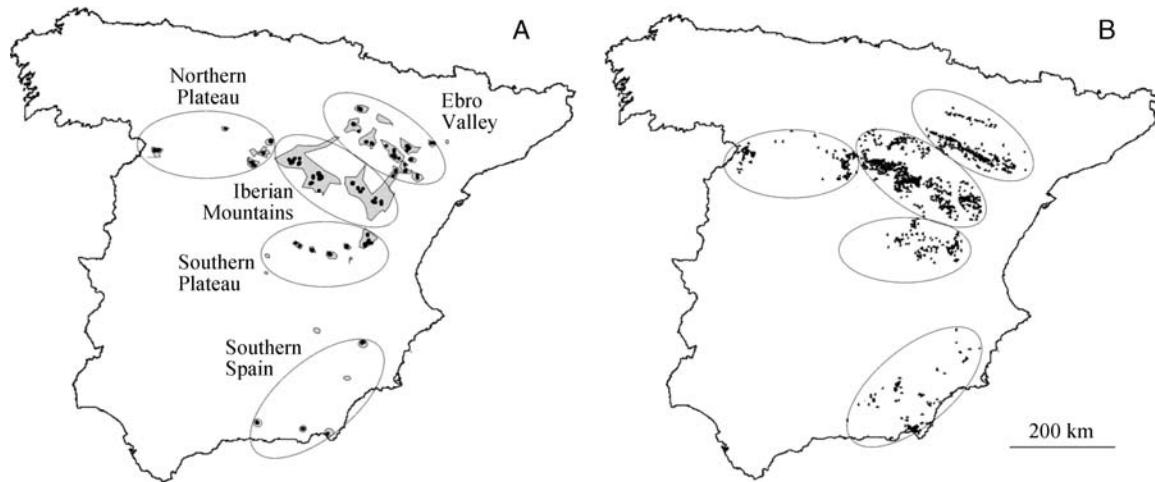


FIG. 1. (A) Locations of the Dupont's Lark males recorded in this study (black points), their grouping into broad geographic areas (ellipses), and known distribution of the species in Spain (gray shaded areas) (modified from Garza et al. [2003]). Geographic areas were not arbitrarily defined, but correspond to well-differentiated topographic, climatic, and population characteristics. (B) Potential distribution of Dupont's Lark derived from a Bayesian model of presence/absence data built in each geographic area with topographic, climatic, and land use descriptors; black areas shows $\geq 75\%$ probabilities of occurrence.

Catalunya (G. Bota, *unpublished data*), and a couple of populations of fewer than 10 territories in Castilla-La Mancha (V. Garza, *unpublished data*) (Fig. 1). These marginal areas were also visited during this study, but we did not record vocal activity.

In March–June and September–November 2004 we tape-recorded Dupont's Lark males throughout the whole species distribution in Spain (Fig. 1). Males were recorded in their territories, and their positions established by means of a Global Positioning System Garmin eTrex Navigator (Olathe, Kansas, USA). The identification of territories was facilitated by extensive information from territory-mapping work in most of the study areas (Garza et al. 2003, Tella et al. 2005; V. Garza, J. Manrique, D. Serrano, F. Suarez, J. L. Tella, and M. Vögeli, *unpublished data*). Birds were recorded with a Sony TC-D8 DAT (Tokyo, Japan) recorder and a Sennheiser ME67 (Wennebostel, Germany) microphone (frequency response 50–20 000 Hz). Most of the sampled males were not marked, but they were recorded in their territories during a single visit only, thus avoiding the problems of individual identification in successive days.

Sound analyses

Dupont's Lark males emit several vocalization types, the most common being the complex song (uttered almost exclusively in spring), the territorial call, and the warning call (the last two also heard outside the breeding season) (Cramp 1988, Laiolo and Tella 2005, Laiolo et al. 2005). We concentrated here on territorial calls, which can be classified in six broad types: three ending with a tonal element (tonal whistles) and three made up of pure notes of constant pitch (whistles) (Fig. 2 shows typical spectrograms). Each individual gave 1–3 call types during call bouts, on average 2.02 ± 0.5 types per individual (mean \pm SD). When more than

one call type was uttered, variants were regularly alternated; for example, when individual repertoire included call types A, B, and C, the typical sequence was A - B - C - A - B - C, etc. During field surveys, we tape-recorded the vocalizations of almost 500 males (approximately one-third of the Spanish population). Territorial calls were uttered by 281 birds, but we restricted the analysis to the 255 individuals that produced at least three calls to assure that we recorded the individual's whole repertoire. In fact, birds uttered their whole repertoire after giving 2.4 ± 0.06 calls (mean \pm SE; only birds uttering >5 calls were considered for this estimate). This value remained constant irrespective of the number of calls recorded (differences among classes of individuals for which 5–10, 11–20, 21–30, and >31 calls were recorded: $F_{3,151} = 0.96$, $P = 0.4$). The number of males recorded varied among geographic areas due to their variability in population sizes (Table 1).

Sound analyses were carried out with Avisoft SASLab Pro (Version 3.91) Software by Raimund Specht (Berlin), performing a Fast Fourier Transform (sampling frequency 22 050 Hz, FFT length 512, time resolution 8.9 ms, frequency resolution 43 Hz). Bartlett Window Function was used to suppress spectrum distortion. Acoustic characteristics were measured in the time domain on envelope (displayed as a two-dimensional graph of sound amplitude against time) and in frequency domain on fast Fourier transform mean spectra (amplitude against frequency). For each call type, we measured the overall duration and the duration and frequency values of each note. In the case of the last note of tonal whistles (Fig. 2), we measured the peak carrying frequency and the fundamental frequency (difference between two multiple frequency bands). Overall, measurements were taken on 2391 calls (Table 1).

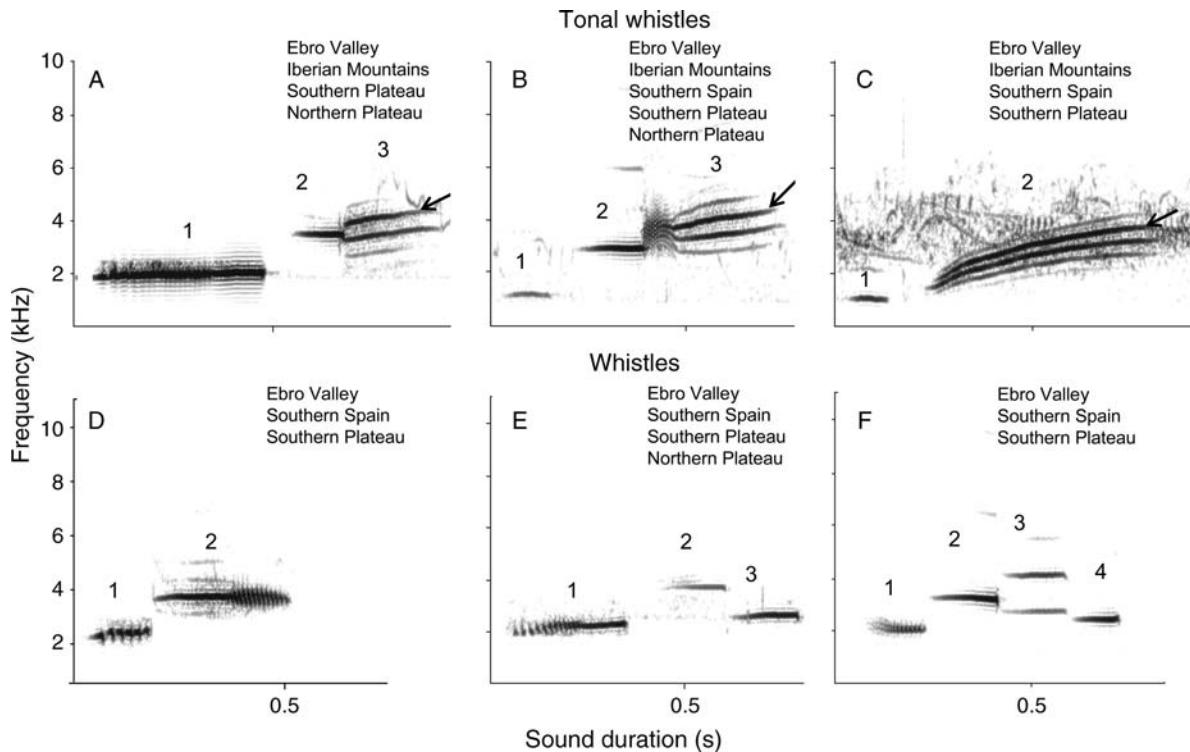


FIG. 2. Spectrograms representing the six broad types of territorial calls of Dupont's Lark. In the time domain of all calls, we measured overall call duration and duration of each note (notes are numbered). In the frequency domain, we measured the frequency of each note in whistles (types D, E, and F), and the frequencies of all notes except the last one in tonal whistles (A, B, and C). In note 3 of calls A and B and note 2 of call C, we measured the fundamental frequency (difference between two multiple-frequency bands) and peak carrying frequency (arrow). The areas where each call type was uttered are also listed.

We first carried out a prior assessment of intra-individual variability, using a sample of seven neighbor males from Llano de Visiedo (the Iberian Mountains), each giving 11–29 calls. By using birds from a single locality, we ruled out any effect of geographic differentiation on among-individual variation. Repeatability analyses (Lessells and Boag 1987) were conducted for each call variable to assess whether interindividual variation is larger than intra-individual variation in at least some variables, a prerequisite for individual distinctiveness of close neighbors (e.g., Jouventin 1982). Repeatability was high for all call variables (range of intraclass correlation coefficients $r = 0.67$ – 0.99 , all P values < 0.001). We can therefore conclude that males gave highly repetitive calls, and even a small sample could be adequate to characterize them. Moreover, a study on marked birds suggests that individuals maintain their territorial calls in different seasons and years (P. Laiolo, M. Vögeli, J. L. Tella, and D. Serrano, unpublished data).

Variation at the levels of individual, population, and geographic area

We calculated individual mean values of spectro-temporal variables, and then built an “individual \times acoustic variable” matrix with 0 values entered for

spectro-temporal variables of call types that were not uttered by an individual. Acoustic variability was quantified in terms of differences in number of call types (repertoire size) and in terms of Euclidean distances of acoustic variables between individuals (call dissimilarity). We tested for acoustic differences following a hierarchic approach that involved different scales: from the individual, to population, to broad geographic areas.

At the individual scale, we tested for differences in individual repertoire size and in pairwise individual dissimilarities between broad geographic areas.

At the population level, we tested for among-areas differences in population repertoire size and within-population acoustic dissimilarities. The latter was calculated in each population by averaging acoustic Euclidean distances between individuals to derive a measure of intrapopulation dissimilarity. As Southern Spain hosts very few and small populations (Fig. 1, Tella et al. 2005), we were not able to get enough samples there for conducting analyses at the population scale. Therefore, we could only test for differences between the remaining four geographic areas, entering in the analysis 15 populations with 6–26 recorded individuals each.

At the broad geographic scale, we verified differences in overall-area repertoire size. To test whether any

TABLE 1. Acoustic and landscape characteristics of the five broad geographic areas.

Geographic area characteristics	Iberian Mountains	Ebro Valley	Southern Plateau	Northern Plateau	Southern Spain
Indices of habitat patchiness					
Mean patch size (ha)	1712	1160	903	929	1005
Distance between nearest neighbor suitable patches (m)	2127.8	3513.9	3893.5	4827.5	9073.4
Total core area (ha)	203 320	79 988	33 228	55 960	39 316
Mean core area per patch (ha)	1007	769	475	589	666
Overall suitable habitat (%)	10.2	4.2	2.1	2.8	1.6
Mean landscape connectivity [†]	1.0	0.7	0.4	0.4	0.3
Acoustic data					
No. individuals recorded	85	98	33	25	14
No. calls recorded	687	966	362	247	129
Repertoire size per individual	1.96	2.12	2.00	1.88	1.85
Pairwise dissimilarities between individuals (Euclidean distances)	6.64	9.10	9.21	11.58	9.28
Observed overall repertoire size (no. call types)	3	6	6	3	5
Expected overall repertoire size [‡]	3.0	5.0	5.0	2.9	5.5
Confidence intervals (95%) of expected repertoire size	3.0–3.0	3.5–6.4	4.3–6.6	2.5–3.4	5.0–5.0
Repertoire size per population [§]	3.0 (5)	3.6 (5)	2.7 (3)	2.0 (2)	
Mean acoustic dissimilarities within population	6.05	7.28	5.75	5.68	

[†] We divided landscape fragmentation indices by the maximum values recorded for each index, and then averaged the four proportions in each area to derive a mean value of landscape connectivity for each area. The latter measure varies from 0 (minimum relative connectivity) to 1 (maximum relative connectivity).

[‡] As derived from rarefaction of the largest samples to the smallest.

[§] The number of distinct populations considered is in parentheses.

differences in the number of call types represented actual differences among areas, and not just sampling differences derived from the different number of individuals recorded (Table 1), we condensed the largest samples down to the smaller, and then compared the expected overall number of call types (Hurlbert 1971, Heck et al. 1975). We used EcoSim Version 7.19 (*available online*)² for computer sampling the algorithm of rarefaction in which a specified number of individuals was randomly drawn from a call sample (Gotelli and Entsminger 2001). The process was repeated 1000 times to generate a mean and a low and high bound for a 95% confidence interval of number of call types. When 95% confidence intervals overlapped, we assumed that these were not significantly different one from another.

Hierarchical components of acoustic diversity

The repertoire size of a broad geographic area (area acoustic diversity) can be partitioned into three components: individual diversity, within-population diversity, and among-population diversity. We calculated (1) the relative contribution of individual diversity to area diversity by dividing mean individual repertoire size by overall area repertoire size; (2) the relative contribution of within-population diversity as the difference between population repertoire size and mean individual repertoire size, divided by area repertoire size; and (3) the contribution of among-population diversity to overall repertoire size as the difference between area repertoire size and mean population repertoire size, divided by area repertoire size. We thus regarded call type partitioning as analogous to estimating the number of species at

different spatial scales in a community: α , β , γ diversity (Lande 1996, Laiolo 2005). As in the case of analyses at the population scale, we could not include Southern Spain for measuring components of acoustic diversity.

Habitat suitability model, quantification of landscape patchiness, and pairwise geographic distance measures

In order to quantify the magnitude of landscape patchiness, we built a predictive model of Dupont's Lark distribution. To sharpen the precision of the model and account for the strong geographic differences in climate and topography, we modeled the distribution of the species in the five delimited areas separately (Fig. 1). We used presence points derived from this study; in order to minimize autocorrelation, we based the model on 173 locations of territories set at a nearest neighbor distance >500 m (Iberian Mountains, 72 points, Ebro Valley, 43 points, Southern Plateau, 28 points, Northern Plateau, 19 points, Southern Spain, 13 points). Another 39 random locations were used to evaluate the model. Eighty pseudo-absence points were generated at random in each of the areas (Hirzel et al. 2001), using the extension ANIMAL MOVEMENT ANALYSIS (Hooge et al. 1999) for ArcView version 3.1 (ESRI 1998). The environmental variables used to predict habitat suitability were derived from a CORINE land-use/land-cover digital map (CEC 1991; map resolution = 100-m): the original 44 categories were pooled in broad groups (arboreal vegetation, natural grassland, sclerophyllous vegetation, sparsely vegetated areas, arable land); DEM digital elevation model: altitude and slope (100 m resolution); climatic digital maps: mean annual temperature and rainfall (Bustamante 2003, Seoane et al. 2003; 1-km resolution). A buffer ring of a 250 m

² <http://garyentsminger.com/ecosim/index.htm>

radius around each point was created and clipped with digital maps in order to extract the environmental predictors of presence and random buffers.

We used a Bayesian approach to statistically formulate the model in keeping with Aspinall (1992) and Hill et al. (1997). Models based on Bayesian statistics combine a priori probabilities of observing species with their probabilities of occurrence conditional to values of each environmental predictor (Guisan and Zimmermann 2000). First we calculated the relative frequencies of presence and random points within discrete classes of each predictor (Appendix). These frequencies are the conditional probabilities of presence $p(y|x_i)$ (i.e., the probability of observing y from the body of data x if the hypothesis of presence is true) and absence $a(y|x_i)$ (i.e., the probability of observing y from the body of data x if the hypothesis of absence is true). We then tested for differences in conditional probabilities of presence and absence with χ^2 tests; significance levels were used to decide which descriptors entered in the model. We set the prior probabilities of presence $p(x)$ and absence $a(x)$ to be modified by the calculated conditional probabilities at 0.5; in doing this, we assumed an equal probability of presence and absence (Aspinall 1992). The descriptor data sets were combined by means of Bayes' theorem to calculate the probabilities of presence $p(x|y)$:

$$p(x|y) = \frac{p(y|x_i) \times p(x)}{p(y|x_i) \times p(x) + a(y|x_i) \times a(x)}$$

The resulting percentage of correct classification of presence data ranged from 75% to 100%, and that of pseudo-absence ranged between 90% and 95%. The descriptors, conditional probabilities, and predictive abilities of the five models are also listed in the Appendix. Altogether, predictions largely agreed with the previous information available on habitat selection at smaller scales (Garza and Suárez 1990, Seoane et al. 2006, Garza et al., *in press*). The species strongly avoids cultivated and forested areas, and selects rather flat areas covered by scattered and short steppe vegetation, sited at varying altitude and climatic stages depending on the broad geographic areas occupied (Appendix). We calculated the probabilities of occurrence for each 2×2 km square in the five geographic areas, and assumed that habitat suitability for the Dupont's Lark could be adequately represented by P values >0.75 (Fig. 1). In fact, 69.2% of the points held to validate the model eventually fell within the predicted distribution. Therefore, we feel our models are good enough to derive a map for the distribution of suitable habitats for Dupont's Lark at the broad scale required in this study (Fig. 1).

We used FRAGSTATS extension for ArcView (McGarigal and Marks 1995) on the five possible distribution maps to calculate the following indices of landscape structure and fragmentation: mean size of a

patch of suitable habitat, mean nearest neighbor distance between patches, total core area, mean core area per patch, and percentage of suitable habitat. The absolute sizes of suitable patches and core areas obtained may have little value per se, since these areas depend on the grain of the models (in our case, grids of 2×2 km squares). However, they can still be used to highlight relative differences among geographic areas. All these indices were then combined to obtain an index of mean landscape connectivity by transforming the raw values of the five indices to relative proportions (dividing each value by the maximum recorded in the five areas) and averaging them. As nearest neighbor distances varied inversely with respect to patch and core area size, in the case of distance values we expressed the proportion as $1 - (\text{distance}/\text{maximum distance})$. By focusing on proportions instead of raw values, we could test for overall differences among areas in landscape connectivity irrespectively of the metrics used (meters or hectares). The resulting index varied between zero (minimum connectivity, maximum patchiness) and one (maximum connectivity, minimum patchiness).

We used the habitat suitability map (Fig. 1) with exact P values for each square to derive a friction map for the whole species distribution. Given that the Dupont's Lark strongly avoids habitats other than natural, flat steppes throughout its annual cycle, this map would represent the cost of dispersal movements for birds through the landscape. This cost was expressed as a function of the probability of occurrence in each square $\text{COST} = (1 - \text{probability of occurrence}) \times 100$, which is determined by habitat suitability.

Within each broad geographical area, we calculated three distance measures between calling individuals: (1) Euclidean geographic distance, i.e., the length of the straight line separating one individual from another; (2) length of the least-cost path, i.e., the distance between individuals, assuming that they maximize the use of suitable habitats to move from one location to another (Fig. 1); and (3) least-cost distance, i.e., the cumulative cost distance of the least-cost path. This is the minimum distance between individuals expressed in cost units rather than in length units (based on the probability of occurrence in each square). The latter two measures were extracted with the PATHMATRIX extension for ArcView (Ray 2005).

Identification of spatial patterns: spatial autocorrelation analysis and Mantel statistics

Spatial autocorrelation analysis was performed to measure acoustic dissimilarity between individuals as a function of geographic distance (Sokal and Neal 1978). By using discrete distance classes, we applied a permutation procedure using Monte Carlo simulations to test for significant deviation from spatial random distribution at each distance class (Manly 1997). Each permutation consists of a random redistribution of data over the spatial coordinates of the sampled points; for

each of the spatial distance classes, observed values were compared with the distribution obtained after 1000 permutations. A 95% CI was constructed, allowing us to infer statistical differences between observed and random values (Streiff et al. 1998). We performed autocorrelation analysis with SGS software (Degen et al. 2001) by expressing pairwise acoustic dissimilarity in terms of city-block distances (Deichsel and Trampisch 1985).

In order to test for the influence of habitat fragmentation on vocal variability, we calculated correlations among an Euclidean dissimilarity matrix of acoustic variables (dependent matrix) and Euclidean geographic distances, lengths of the least-cost path, and least-cost distances (independent matrices). To control for the covariation of the independent matrices, we used a partial Mantel test procedure (Smouse et al. 1986), with probabilities deriving from running 1000 iterations of the data set.

RESULTS

Landscape patchiness

The five broad geographic areas showed differences in the indices of habitat patchiness, with the Iberian Mountains showing the greatest relative landscape connectivity and Southern Spain the least (Kruskal Wallis ANOVA, $H_{4,25} = 13.8$, $P = 0.008$). The largest patches of suitable habitat were found in the Iberian Mountains, and the smallest in the Southern and Northern Plateaus. Southern Spain showed the longest distances among suitable patches and, together with the Southern Plateau, hosted the most irregularly shaped patches (Table 1).

Differences in acoustic variability between geographic areas

Individual scale.—Individual repertoire size was similar in the five geographic areas and averaged two call types per individual (range 1.88–2.12 calls; Kruskal-Wallis ANOVA, $H_{2,255} = 6.94$, NS) (Table 1). Nonetheless, geographic areas differed in mean acoustic dissimilarities between individuals: birds in the Northern Plateau showed the greatest pairwise acoustic dissimilarities, whereas those from the Iberian Mountains had the lowest dissimilarity values (Table 1). These differences were significant even when accounting for variability in the distances existing between individuals (one-way ANCOVA with geographic distance as covariate: $F_{4,9236} = 280.8$, $P < 0.001$).

Population scale.—Populations from the Ebro Valley showed the richest call repertoire (on average, 3.6 types per population), whereas those from Northern Spain uttered the poorest (2.0 types), with the Iberian mountains and the Southern Plateau showing intermediate values (Kruskal-Wallis ANOVA, $H_{3,15} = 7.9$, $P < 0.05$; Table 1). Notably, all populations from the Iberian Mountains uttered the whole-area repertoire, whereas other populations only uttered a portion of the

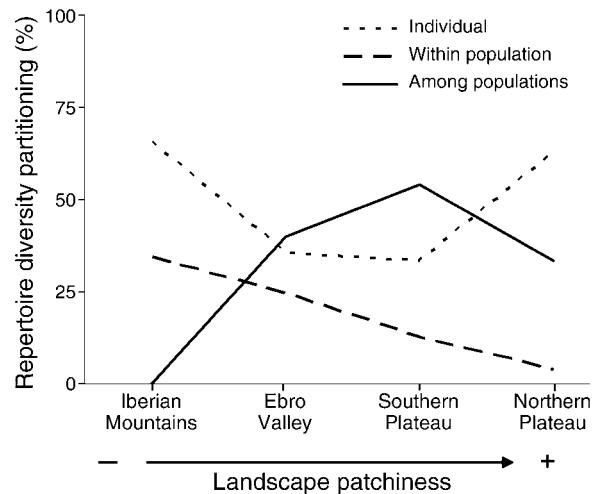


FIG. 3. The percentage relative contribution of individual, within-, and among-population diversity to overall acoustic diversity of four broad geographic areas (diversity is expressed in terms of repertoire size).

call pool of their area (average percentage of the area repertoire uttered by populations: Iberian Mountains, 100%; Ebro Valley, 60%; Northern Plateau, 67%; Southern Plateau, 44%). When considering mean Euclidean acoustic distances within populations, differences between geographic areas were no longer significant (Kruskal-Wallis ANOVA, $H_{3,15} = 1.3$, NS).

Geographic-area scale.—In order to test for differences in repertoire size among the five areas, we carried out rarefaction analyses by standardizing the number of call types per area to the smaller sample, which was that of Southern Spain (14 individuals and 129 calls). Overall repertoire size of the Ebro Valley, Southern Spain, and the Southern Plateau was significantly greater than that of the Northern Plateau and the Iberian Mountains, since the expected repertoire size of the latter two areas fell outside the lower confidence interval of the former three (Table 1).

Hierarchical components of acoustic diversity

When considering the relative contribution of individual, within-, and among-population diversity to overall geographic-area diversity (in terms of repertoire size), within-population diversity tended to decrease and among-population diversity to increase in a gradient of increasing landscape patchiness (Fig. 3). The relative contribution of individual diversity, however, was always high and unrelated to changes in patchiness among geographic areas.

Relationships between landscape features and call variability

The territorial call showed a significant spatial pattern of diversification with distance throughout Spain: observed call dissimilarities were significantly lower than those expected by chance for distances <80 km,

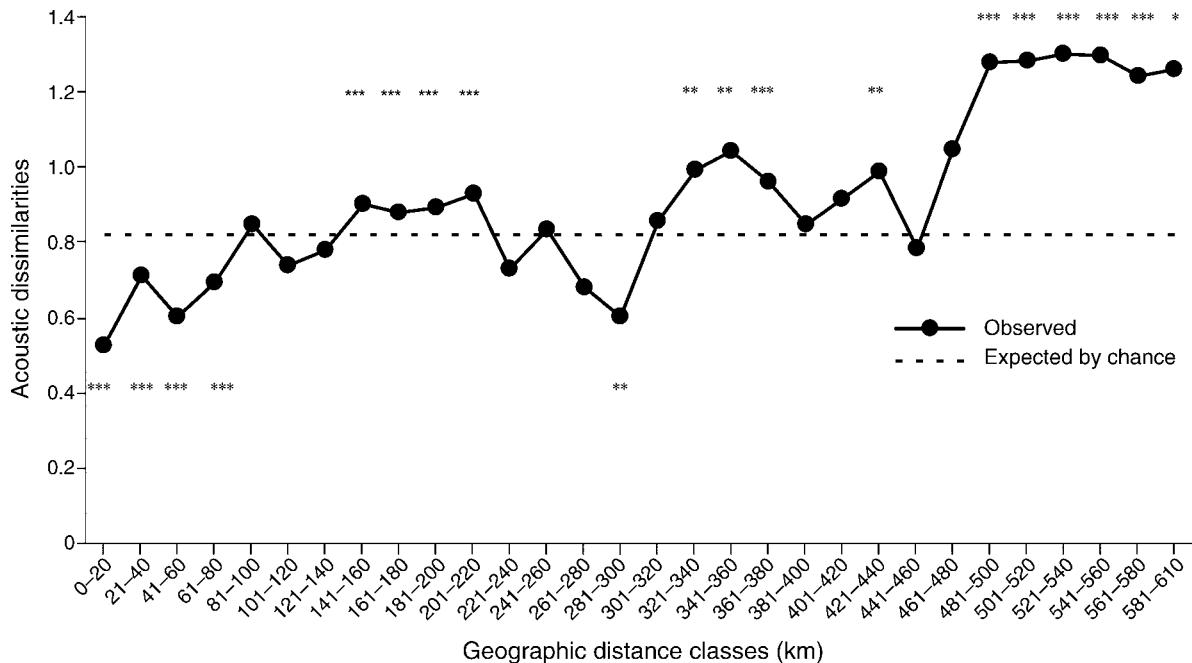


FIG. 4. Relationship between dissimilarities in Dupont's Lark territorial calls and geographic distance classes across Spain. We used a permutation procedure (Monte Carlo simulations) to test significant deviation from spatial random distribution at each distance class (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

and often significantly higher than expected for longer distances (Fig. 4). There was, however, a high degree of scatter between plotted points in Fig. 4, which resulted from clumping data from five geographic areas that greatly differ in their landscape structure. When each area was analyzed separately, no clear relationship resulted between call dissimilarities and geographic distance in the Iberian Mountains. The Ebro Valley, Southern Spain, and Northern and Southern Plateaus showed significant trends but differently shaped scatterplots (Fig. 5). In all these areas we found negative dissimilarity coefficients (lower than those expected by chance) for distances < 20 km, whereas significant positive coefficients (greater than those expected by chance) occurred at different distance classes. In Ebro Valley, call dissimilarities were significantly positive for distances > 100 km; when these distances were reduced to 80 and 40 km in the Southern and Northern Plateaus, respectively, they resulted in a progressively steeper increase of acoustic dissimilarities with distance when increasing the magnitude of patchiness. Southern Spain is at the extreme of the isolation gradient, but the minimum distances at which call dissimilarities become significantly positive cannot be calculated there, given the current long-distance isolation of its populations (Fig. 5).

Call variability in Dupont's Lark was related not only to isolation by distance but also to isolation by habitat unsuitability. The relative contribution of these two isolation processes also varied between geographic areas following a gradient of habitat patchiness. Isolation by

habitat unsuitability was stronger (i.e., correlation coefficients calculated with the Mantel test increased) the larger the patchiness of the areas; isolation by distance simultaneously increased its correlation. There is no indication of isolation by distance in the least fragmented area, the Iberian Mountains (Mantel test not significant for Euclidean distances; $P = 0.2$). In this area, the coefficients of least-cost distance or length of the least-cost path (indicators of isolation by habitat unsuitability) were significantly related to call dissimilarities (Mantel $r = 0.29$ and 0.23 , respectively; $P < 0.01$ for both measures). In highly fragmented areas (the Ebro Valley, Southern Spain, and Northern and Southern Plateaus), the three measures of isolation showed significant correlation coefficients, with the indicators of habitat unsuitability often showing higher values than those of straight-line distance (Mantel r for Euclidean distances ranging from 0.20 to 0.77 ; $0.05 > P > 0.001$; Mantel r for the length of the least-cost path: 0.31 – 0.73 ; $P < 0.001$, Mantel r for least-cost distance: 0.23 – 0.81 ; $0.01 > P > 0.001$).

DISCUSSION

Magnitude of landscape and population fragmentations

Our habitat suitability model points out marked geographic differences in the magnitude of patchiness and in the availability of suitable fragments for the Dupont's Lark throughout Spain. These differences are likely to be responsible for the divergences in species abundance among geographic areas. The largest frag-

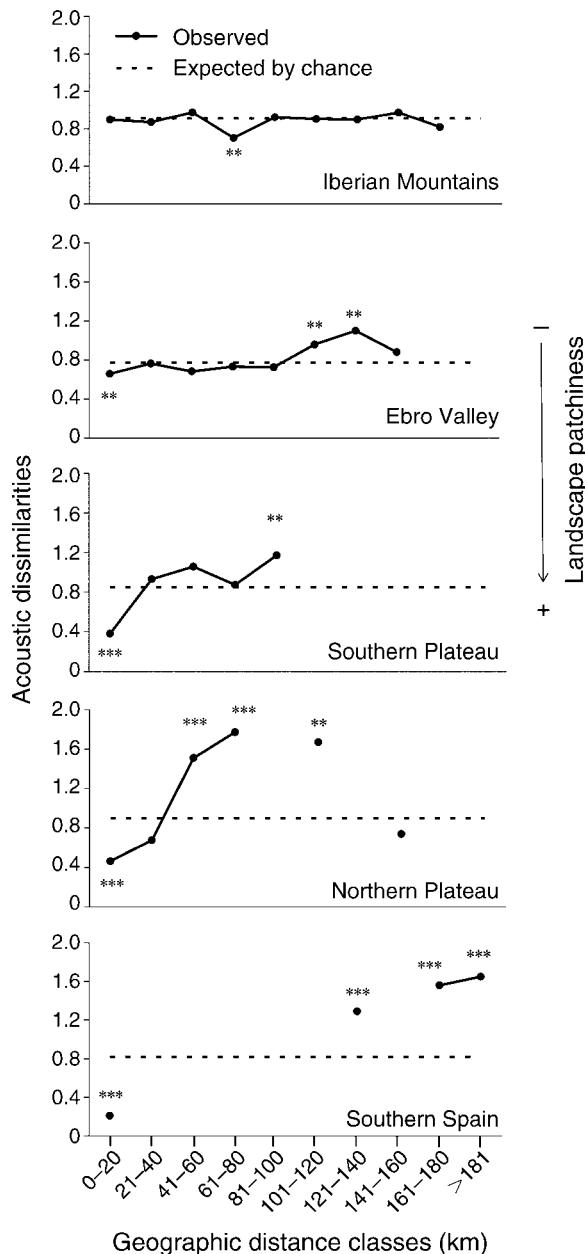


FIG. 5. Relationships between acoustic dissimilarities and geographic distance classes in the five geographic areas. We used a permutation procedure (Monte Carlo simulations) to test significant deviation from spatial random distribution at each distance class (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). The observed trends of Northern Plateau and Southern Spain are presented as broken lines because of missing distance classes.

ments and the greatest proportion of suitable habitat are found in the Iberian Mountains, which also host the bulk of Iberian populations of Dupont's Lark (Garza et al. 2003a). Fragments in the Ebro Valley are smaller, but still partially connected; this is the second numerically important area for the species in Spain (Tella et al. 2005). Southern Spain, the Northern Plateau, and, to a lesser extent, the Southern Plateau, show extreme

patchiness levels with small portions of proper patches isolated by a matrix of unsuitable habitat (Fig. 1). In Southern Spain and the Northern and Southern Plateaus, anthropogenic habitat loss has reduced the species distribution to a few populations, all numerically very scarce. Disappearing from many sites, steppe cover is also decreasing here, including the fragments that are still inhabited by the species (P. Laiolo and J. L. Tella, unpublished data).

Isolation by geographic distance and by landscape unsuitability

Call differentiation shows a clear pattern of isolation by distance, increasing at long geographic distances (Fig. 4). The large geographic scale of this study makes the observed trend quite realistic: maximum interindividual distance is 610 km across Spain, whereas it can reach 245 km within zones. These are long pathways to cross for a small, reluctant-to-fly, sedentary passerine, which therefore might restrict its main dispersal (and that of its calls) to shorter distances. Isolation by distance patterns are quite common in the acoustic communication systems of vertebrate species (Castellano et al. 2000, Slabbekoorn et al. 2003, Eiler and Banack 2004).

In the Iberian Mountains, there is no clear isolation by distance pattern. Conversely, birds from the Ebro Valley, Southern Spain, Northern and Southern Plateaus show both long-distance call differentiation and short-distance similarities, indicating that there is not a fixed spatial range of acoustic similarities (differences increase progressively, and acoustic divergence does not stabilize at long distances). The increase of acoustic dissimilarities with distance is steeper in highly fragmented areas (Fig. 5), suggesting that isolation by distance is not the sole mechanism involved in population differentiation and that landscape configuration plays an important role in it. This finding is confirmed by the significant relationships among interindividual acoustic dissimilarities and the measures of landscape connectivity (least-cost distance and length of the least-cost path), while controlling for the more intuitive effect of the distance separating them. Hence, fragmentation and habitat isolation appear to force bird movements through pathways of suitable habitats, thus constraining the free circulation of calls.

To our knowledge, this is the first large-scale study using indirect indicators (behavioral or genetic traits) showing that incorporating landscape structure in distance measures may allow a better detection of isolation mechanisms, even when straight-line geographic distance fails to explain differentiation patterns (the case of the Iberian Mountains). So far, most literature on spatial autocorrelations has simply pointed to straight-line distances between populations or individuals (Diniz-Filho and Telles 2002, Manel et al. 2003). Only a few small-scale studies have addressed the connectivity of fragments to better approximate an isolation measure to be correlated with genetic diversity

(Vos et al. 2001, Coulon et al. 2004). Previous studies, moreover, did not empirically quantify isolation by means of habitat suitability models. Predictive models statistically relate the geographic distribution of species to their environment, which includes vegetation, land use, topographical and climatic components (Guisan and Zimmerman 2000). These models are more rigorous and informative than many other subjective quantifications of habitat suitability (Peters 1991), and thus can be used as an effective tool to measure the costs of movement throughout the landscape, as we have shown here.

Consequences of habitat patchiness and isolation on acoustic diversity

By considering these results, it could be stated that habitat patchiness increases call dissimilarities at large geographic scales. However, at which level is acoustic diversity increasing: at the individual or population level or both?

At the individual scale, males from patchy areas utter the same number of call types as those from more continuous habitats; thus we cannot attribute the broad differences in repertoire size between areas to differences in individual faculties of uttering a rich repertoire.

Conversely, our results suggest that patchiness better results in a reduction of acoustic diversity within populations and a parallel increase in differentiation among populations (Fig. 3). In Ebro Valley, where patchiness is still associated with good fragment connectivity, we recorded the greatest richness in call pool per population (Table 1). Here, landscape fragmentation might promote population acoustic divergence, and landscape connectivity ensures the spread of call variants among populations. In the Northern Plateau, where unsuitable habitats represent a greater barrier (Fig. 1), isolated populations might diverge and develop their own call repertoires. However, successive mixing could be limited by the lack of connectivity, thus resulting in a lower number of call types per population. In the Iberian Mountains, populations utter fewer call types than those in the Ebro Valley, but share the call pool of nearby populations, suggesting that a strong homogenizing effect occurs when barriers are limited. All in all, these results imply that intermediate patchiness levels can promote acoustic differentiation, but extreme patchiness ultimately erodes call diversity within populations in a process that could be viewed as analogous to genetic drift. In small and isolated fragments, call patterns might be lost by accident, and drift may contribute to reduce the diversity within a population and accelerate differentiation among populations (Lynch 1996). This would also explain why populations in largely fragmented areas only utter a portion of their zone repertoire, whereas in the Iberian Mountains all populations share the same pool of calls.

If dispersal between populations is largely constrained by habitat unsuitability and distance, both demographic and environmental stochasticity may provoke the even-

tual extinction of small and isolated populations. The great amount of hostile habitat coupled with the scarce number of populations could then limit recolonization to a great extent (Fahrig and Merriam 1994, Bascompte et al. 2002). From a conservation point of view, management efforts should focus on creating corridors and/or stepping stones between populations, depending on the resistance of the surrounding matrix (Baum et al. 2004), rather than solely on conserving habitat availability to maintain the viability of the more isolated populations.

Landscape bioacoustics vs. genetics

Both theoretical and applied implications can be drawn from these results. This study shows that acoustic features can be used to approximately track animal dispersal processes, thus widening the applications of bioacoustics in a population biology context.

Most songbirds learn their song either before natal dispersal or from their neighbors during their first breeding season (Kroodsma 1982). If learning occurs before dispersal, birds will carry their vocalizations with them when they move; if birds learn new calls after they move to a new area, acoustic elements will not diffuse even if populations are in contact (Lynch 1996). The latter case occurs with the Dupont's Lark's complex song (Laiolo and Tella 2005). However, the maintenance of territorial call features over long distances (the same call types are also audible in northern Africa; P. Laiolo and J. L. Tella, *unpublished data*) suggests that this vocalization is learned before dispersal. In most passerines, song learning occurs through male-male transmission (Kroodsma 1982). As a consequence, acoustic studies might highlight male movements, which are largely undetected by genetic studies that address matrilineal or biparental transmission. In light of this, the study of animal communication cannot be viewed as an alternative but a source of complementary information to genetic studies, given that it brings evidence of phenomena that are currently undetectable from molecular data.

This study shows that landscape isolation and fragmentation can influence the cultural evolution of natural populations, not just their genotypic or morphological composition. We suggest that acoustic differentiation patterns might foresee genetic processes and allow an earlier detection of isolation processes occurring in local populations, taking into account that vocalizations are one of the most powerful isolating mechanisms known, due to their rapid evolution, and their role in species recognition and mate choice (O'Loughlen and Rothstein 1995, Grant and Grant 1996, 1997). Bioacoustics might therefore detect the effects of natural patchiness and/or anthropogenic fragmentation when molecular markers might still be unable to infer gene flow in case of minimal genetic differentiation (Pearse and Crandall 2004). We stress the importance of carrying out acoustic research in heterogeneous landscapes, to be coupled and compared with genetic evidence, in order to verify whether the interplay of different disciplines might

increase our ability to properly study and subsequently manage species in fragmented landscapes.

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APPENDIX

A table showing classes of environmental predictors that showed significant differences between conditional probabilities of presence and pseudo-absence (random points), as tested by chi-square tests, and a figure of a friction map example (*Ecological Archives* E087-070-A1).